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Expanded Simulation Models (Version 3.0) for Growth of the Submersed Aquatic Plants American Wildcelery, Sago Pondweed, Hydrilla, and Eurasian Watermilfoil

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PURPOSE: This technical note describes modifications of simulation models for growth of four submersed aquatic vegetation (SAV) types, greatly expanding their application potential. The modifications include descriptions of the vegetation responses to daily changes in current velocity and epiphyte shading, and accommodation of daily changes in water level. These models can be used to evaluate key environmental conditions in which SAV would persist under a variety of management scenarios within the watershed. The models are available as stand-alone versions, and can be used singly and in combination with hydrodynamic and sediment transport models.

BACKGROUND: SAV plays an important role in aquatic ecosystems. Desirable species stabilize sediment, ameliorate transparency and regulate nutrient availability in the water column, and serve as habitat and food sources for invertebrates, fish, and waterfowl. Many SAV communities in freshwater and marine environments have experienced dramatic losses during the past three to five decades. Declines are attributed to decreases in water transparency due to anthropogenic influences, but often they have been attributed to other factors such as high water levels, extended draw-downs, changes in current velocity, and epiphyte shading, or to combinations of factors. Once the vegetation is lost from a given locale, increased sediment resuspension and current velocity may place significant constraints on plant recolonization at that site. In contrast, nuisance or invasive SAV species exhibit excessive growth of vegetation, interfering with human utilization of freshwater resources or displacing desirable indigenous communities.

The degree to which SAV influences the ecosystem is proportional to plant mass and depends on plant species and physical and chemical factors. Therefore, predictions of the environmental impact of management measures concerning the aquatic system in which the SAV grows should be based on accurate estimates of (1) plant species, mass, and its pertinent physiological properties, (2) the plants' contribution to the various food chains, and (3) the contribution of the plants' decay to biogeochemical cycling and oxygen regime. Simulation models, which describe SAV responses in terms of biomass dynamics to changes in physical and chemical factors in various climates, can be useful tools for water resource managers because they can be used to evaluate key environmental conditions in which SAV would persist or produce excessive biomass, with ensuing consequences for the systems in which they grow, as impacted by various management scenarios (Carr et al. 1997, Best et al. 2001). Although the number of simulation models for production of monotypic SAV is increasing (e.g. Titus et al. 1975, Best 1981, Collins and Wlosinski 1985, Best and Jacobs 1990, Hootsmans 1994, Scheffer et al. 1993, Herb and Stefan 2003), it is still relatively low compared with that for terrestrial vegetation.

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Simulation models for the biomass dynamics of four common freshwater SAV species have been developed over the last decade, i.e. for *Hydrilla verticillata* (hydrilla; dioecious biotype)-HYDRIL, monoecious *Myriophyllum spicatum* (Eurasian watermilfoil)-MILFO, dioecious *Vallisneria americana* (American wildcelery)-VALLA, and monoecious *Potamogeton* pectinatus[1] (sago pondweed)-POTAM (Best and Boyd 1996, 1999a, 1999b, 2001a, 2001b, 2003a, 2003b, Boyd and Best 1996). These models can be used to simulate plant biomass over a 1- to 5-year period, in climates varying from temperate to tropical. The original versions (1.0) of these models have been developed for shallow freshwater lakes and are limited in their application potential, because they do not accommodate vegetation responses to changes in current velocity and light attenuation by epiphytes and allow only annual changes in water level. These versions are available for users (see 'Product Availability'). For a more general application, including river systems and reservoirs, the inclusion of equations describing the plant responses to changes in current velocity, siltation/epiphyte cover, and to frequent water level fluctuations were needed.

Two models, VALLA and POTAM, were selected for application to sites in the Upper Mississippi River System, both for ecological risk assessment of potential consequences of increased navigation activities, and to explore effects of management scenarios, including 'Pool drawdown' and 'Dam operation for environmental flows.' For this application, the models were recoded to include equations describing vegetation responses to current velocity and riverine epiphyte cover, to accomodate daily changes in water level, and they were recalibrated by the addition of species-characteristic values for the plant responses in the input files. Comparison of the results of the recalibrated model runs with field data indicated that model and field data were in the same range (Best et al. 2005). Although the recalibration and validation of these models have been documented, the executable files have not yet been made available for potential users.

To extend the application potential of both older SAV models (i.e., HYDRIL and MILFO) to the same level as that of VALLA and POTAM, the older models were expanded to include the same equations and calibration data used for VALLA. Thus, all expanded models contain the same process descriptions, but the species-characteristic response values to current velocity and epiphyte cover in the input files of VALLA pertain to *V. americana* and of POTAM pertains to *P. pectinatus*, while those in the input files of HYDRIL and MILFO pertain to *V. americana*-because the required data pertaining to *H. verticillata* and *M. spicatum* could not be retrieved from the literature. Once the pertinent species-characteristic response values of *H. verticillata* and *M. spicatum* become available, they can easily be entered in the input files of HYDRIL and MILFO. All four models were tested for performance by conducting runs at similar sites under temperate and tropical climatological conditions.

[1] *P. pectinatus* has relatively recently moved from the Potamogetonaceae (Voss 1972) into the Stukeniaceae (Crow and Hellquist 2000), and its current taxonomic name is *Stukenia pectinata*. The taxonomic name commonly cited up to 2000 is used in this technical note, since all literature references pertain to the formerly used name of *P. pectinatus* for this plant.

MODEL EXPANSION APPROACH

Example Model. VALLA was chosen to illustrate the model expansions for this technical note. The expanded models (Version 3.0) are available for potential users as executable files, accompanied by pertinent input and weather files (see 'Product Availability'). VALLA is an individual-based, bioenergetics model that simulates growth of a monotypic (single species) SAV community, including roots under the prevailing weather conditions. Model applications in which the Environmental Laboratory (U.S. Army Engineer Research and Development Center) participated include: ecological risk assessment of SAV in the Upper Mississippi River System (Bartell et al. 2000, 2003), habitat suitability explorations for SAV in an Illinois River Pool (Teeter and Best 2003, Best et al. 2004), and ecological resource (SAV and waterfowl) management explorations along the Jangtze River (Wu et al. 2007).

Model Expansions. The models were expanded with equations relating SAV photosynthesis to current velocity, and reducing SAV light interception by epiphyte shading. All arrays were expanded to enable daily calculations for a full year (365 days).

SHORT DESCRIPTION EXAMPLE MODEL AND MODEL EXPANSIONS

Short Description Example Model. VALLA simulates growth of a typical SAV community. In the model, growth is considered to be the plant dry matter accumulation including subterranean tubers, under ample supply of nitrogen and phosphorus, in a pest-, disease-, and competitor-free environment under the prevailing weather conditions. At least one plant cohort waxes and wanes per season in different climates, varying from temperate to tropical. The rate of dry matter accumulation is a function of irradiance, temperature, CO_2 availability, and plant characteristics. The rate of CO_2 assimilation (photosynthesis) of the plant community depends on the radiant energy absorbed by the canopy, which is a function of incoming radiation, reflection at the water surface, attenuation by the water column, by the plant material, and by the epiphytes and leaf area of the community. From the absorbed radiation, the photosynthetic characteristics of individual shoot tips and the pH-determined CO_2 availability, the daily rate of gross CO_2 assimilation of the community is calculated. These calculations are executed in a set of subroutines added to the model. Part of the carbohydrates produced is used to maintain the existing biomass. The remaining carbohydrates are converted into structural dry matter (plant organs). In the process of conversion, part of the weight is lost in respiration. The dry matter produced is partitioned among the various plant organs using partitioning factors defined as a function of the phenological cycle of the community. The dry weights (DW) of the plant organs are obtained by integration of their growth rates over time. The plant winters through tubers in the sediment without or with biomass present. All calculations are performed on a square meter basis. Since environmental factors and plant growth characteristics vary with depth, in the model the water column and associated growth-related processes have been partitioned in 0.10-m depth classes (Titus et al. 1975). Seed formation has not been included in the models, because its role in maintaining existing SAV communities in a temperate climate is minimal. Dispersal and colonization of new habitats by seeds are recognized, important characteristics of SAV. The latter processes, however, are better described using other modeling approaches (based on logistic regression or on descriptions of population dynamics varying in time and in space), as discussed by Scheffer (1991).

General features of the model include:

- Is operational in a one-dimensional (quasi two-dimensional) configuration
- Has 13 state variables
- Provides that the state variable selected may be individually activated or deactivated
- Performs integration using the Runge-Kutta method
- Computes photosynthesis per second and other masses per day
- Operates as a stand-alone version fitted in a FORTRAN Simulation Environment (FSE) shell (Figure 1). Provides binary and ASCII output files, and graphics can be viewed within a user-friendly shell. Coded in ANSI Standard FORTRAN F77.

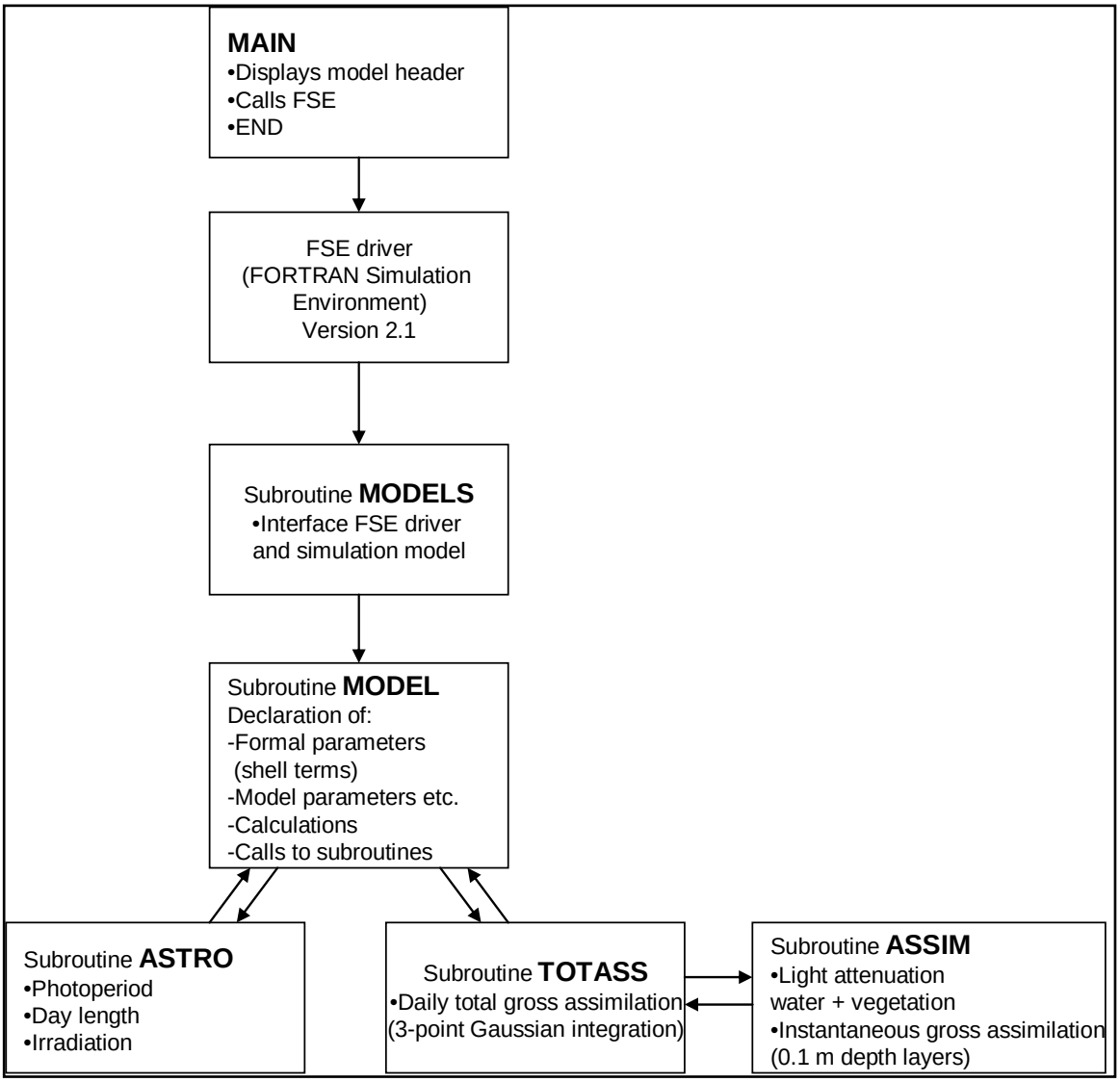

Figure 1. Relational diagram illustrating the organization of an aquatic plant growth model and its subroutines in combination with the FSE shell

VALLA requires the following site-specific inputs:(1) hydrodynamic variables (water depth, current velocity), water transparency, water temperature-if available, which can be entered in the models' input file in ASCII format; and (2) site-specific irradiance and temperature as inputs, which are read from standardized weather files commonly used for agricultural crop growth models. The model can be run using the default values for the plant-specific physiological parameters for periods of 1 to 5 years. Local application of VALLA for sites at which hydrodynamics and sediment transport are modeled is greatly facilitated by interfacing VALLA and both latter model types with a Geographic Integration System (GIS; Black et al. 2003).

State variables. VALLA incorporates 13 state and 2 main auxiliary variables important for plant biomass dynamics, including phenological cycle and carbon flows through various plant compartments (Table 1). Many parameter values of the models are species-characteristic. Tables with parameter values for VALLA, POTAM, HYDRIL and MILFO can be found in Appendix A.

Table 1
VALLA State and Main Auxiliary Variables

State variables
3^{o}C degree-day sum
Developmental phase
Dry weight remobilized carbohydrates
Dry weight leaves (live and dead)
Dry weight stems (live and dead)
Dry weight roots (live and dead)
Dry weight tubers (dormant, newly formed, dead)
Number of tubers (dormant, newly formed, dead)
Main auxiliary variables
Temperature (average daily)
Day length

Central features. Central features of the model are the (1) equation describing instantaneous gross photosynthesis, and (2) link between species-characteristic phenological cycle, physiological processes, and environmental conditions.

Instantaneous gross photosynthesis. Instantaneous gross photosynthesis (*FGL* in g CO_2 m^{-2} h^{-1}) in the models depends on the standing crop per depth layer i (SC_i in g DW m^{-2} $layer^{-1}$), the photosynthesis light response of individual shoot tips at ambient temperature (*AMAX* in g CO_2 gDW^{-1} h^{-1}), the initial light use efficiency (*EE* in g CO_2 J^{-1} absorbed), the absorbed light energy (*IABSL* in $Jm^{-2}s^{-1}$), and temperature (^{o}C, relative function that affects AMAX). The photosynthesis light response of leaves is described by the exponential function

$$FGL_i = SC_i \bullet AMAX \left(1 - \exp\left[\frac{-EE \bullet IABSL_i \bullet 3600}{AMAX \bullet SC_i}\right]\right) \quad (1)$$

The instantaneous rate of gross assimilation over the height of the vegetation is calculated by relating the assimilation rate per layer to the community-specific biomass distribution and by subsequent integration of all 0.1-m-high vegetation layers. The daily rate of gross assimilation is then computed using a three-point Gaussian integration method (Goudriaan 1986, Spitters 1986).

Species-characteristic phenological cycle. The phenology of the plant community, for which the development phase is used as a measure, is modeled as a sequence of processes that take place over a period of time, punctuated by more or less discrete events. Development phase (DVS) is a state variable in the models. The DVS is dimensionless and its value increases gradually within a growing season. The development rate (DVR) has the dimension d^{-1}. The multiple of rate and time period yields an increment in phase. The response of DVR to temperature in the model is in accordance with the degree-day hypothesis (Thornley and Johnson 1990). Calibration according to this hypothesis allows for use of the model for the same plant species at various sites differing in climate (temperature regime). The relationships between the development phase, the day-of-year, and 3 ^{o}C day-degree sum for a temperate climate are presented in Table 2.

Table 2
Relationships Between Development Phase (DVS) of *V. americana*, Day of Year and 3 °C Day-Degree Sum in a Temperate Climate (DVRVT= 0.015; DVRRT= 0.040)

Developmental Phase		Day Number	3°C Day-Degree Sum
Description	**DVS Value**		
First Julian day number → tuber sprouting and initiation elongation	0 → 0.291	0 → 105	1 → 270
Tuber sprouting and initial elongation → leaf expansion	0.292 → 0.875	106 → 180	271 → 1215
Leaf expansion → floral initiation and anthesis	0.876 → 1.000	181 → 191	1216 → 1415
Floral initiation and anthesis → induction of tuber formation, tuber formation and senescence	1.001 → 2.000	192 → 227	1416 → 2072
Tuber formation and senescence → senesced	2.001 → 4.008	228 → 365	2073 → 3167
Senesced	4.008	365	3167

Note: Calibration was on field data on biomass and water transparency from Chenango Lake, New York, 1978 (Titus and Stephens 1983) and climatological data from Binghamton (air temperatures) and Ithaca (irradiance), New York, 1978.

Short Description Model Expansions.

Relation of SAV photosynthesis to current velocity. The VALLA and POTAM models were expanded with equations relating photosynthesis to current velocity. This entailed the following insertions.

- An on/off switch, VELSWT, for activation of the relationship in the input file. The switch is on at the value of 1, and off at the value of 0. Because data on current velocity and epiphyte cover of the SAV are not always available for the sites for which habitat suitability is modeled, these switches can be used to activate the modeled plant response to these factors.

- A species-characteristic factor relating maximum photosynthesis at light saturation to current velocity via a relative, dimensionless, factor (REDAM1≤1) into the ASSIM subroutine of the source code, in which SAV light interception and photosynthesis are calculated. VALLA calibration used data pertaining to the related *E. nuttallii* at low current velocity (Best and Boyd 2003a) and data pertaining to *V. americana* at high current velocity (Best et al. 2005). POTAM calibration used data pertaining to *P. pectinatus* (Best and Boyd 2003a, Chambers et al. 1991). The relationships between current velocity and relative photosynthesis are presented in Figure 2. In these functions the relative photosynthetic rate decreases linearly from 1.0 at a current velocity of 0.07 m s^{-1} to 0 at a current velocity of 0.82 m s^{-1} for *V. americana*, and to 0 at a current velocity of 0.94 m s^{-1} for *P. pectinatus*.

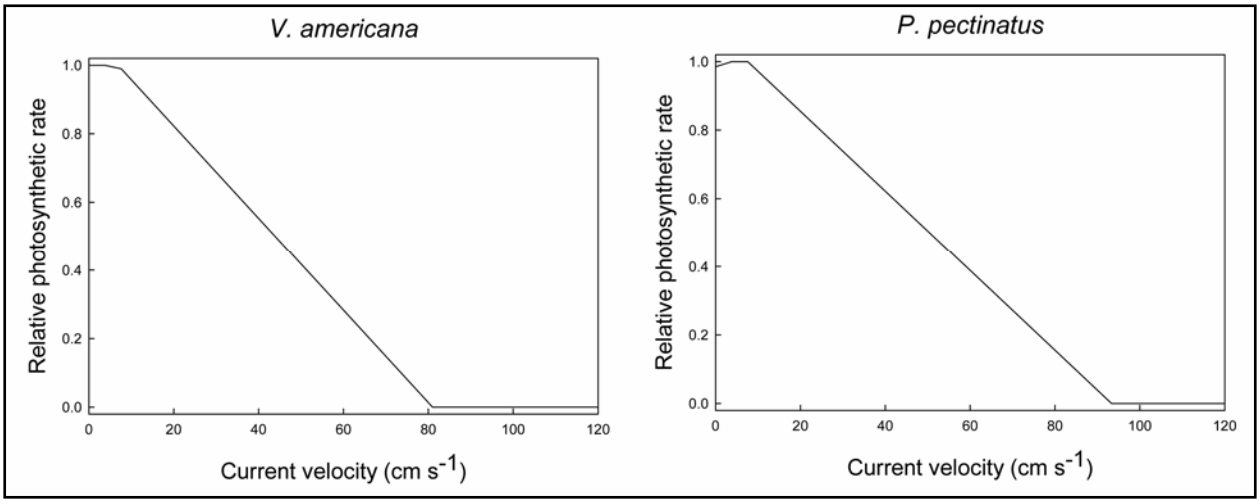

Figure 2. Relationship between current velocity and relative photosynthetic rate used for model calibration

- Measured data on SAV response (REDAM1 as a function of current velocity; in dimensionless units, cm s^{-1}) and current velocity (WVEL as function of Julian day number, in cm s^{-1}, d) in the input file.
    - For VALLA: REDAM1 = 0., 1.0, 3.82, 1.0, 7.636, 0.98973, 82., 0.0, 120., 0.0
    - For POTAM: REDAM1 = 0., 0.98469, 3.82, 1.0, 7.6, 1.0, 93.33., 0.0, 120., 0.0
    - For VALLA: WVEL = 1., 36., ...365., 3 (site 'Turtle Island' in Pool 8, 2001)
    - For POTAM: WVEL = 1., 0., …365., 0. (site 'Lawrence Lake' in Pool 8, 2001)

For both HYDRIL and MILFO the plant response to current velocity and epiphyte shading pertaining to *V. americana* were used, because no such response had been published for *H. verticillata* and *M. spicatum*.

Relation of SAV light interception as affected by epiphyte shading. The VALLA and POTAM models were expanded with equations relating SAV light interception to epiphyte shading. This entailed the following insertions.

- An on/off switch, EPHSWT, for activation of the relationship in the input file. The switch is on at the value of 1, and off at the value of 0.

- A species-characteristic factor reducing SAV light interception by subtracting the fraction of light absorbed by epiphyte cover (EPISHD≤1) into the ASSIM subroutine of the source code, in which SAV light absorption and photosynthesis are calculated. VALLA and POTAM calibration used data pertaining to *V. americana* and *P. pectinatus* in the UMRS Pools 8 and 13 (Best et al. 2005). The relationships between SAV developmental stage and relative epiphytic light interception are presented in Figure 3. In these functions the relative epiphytic light interception increases linearly from 0 at the onset of plant development to a maximum of 0.43 for *V. americana* and 1.0 for *P. pectinatus* at the onset of plant senescence, and decreases again to 0 at the end of plant development.
- Measured data on SAV response (EPHY as function of developmental phase; in dimensionless units, dimensionless units) in the input file.
    - For VALLA: EPHY = 0., 0., 2.0, 0.43, 20.0, 0.0
    - For POTAM: EPHY = 0., 0., 2.0, 1.0, 20.0, 0.0

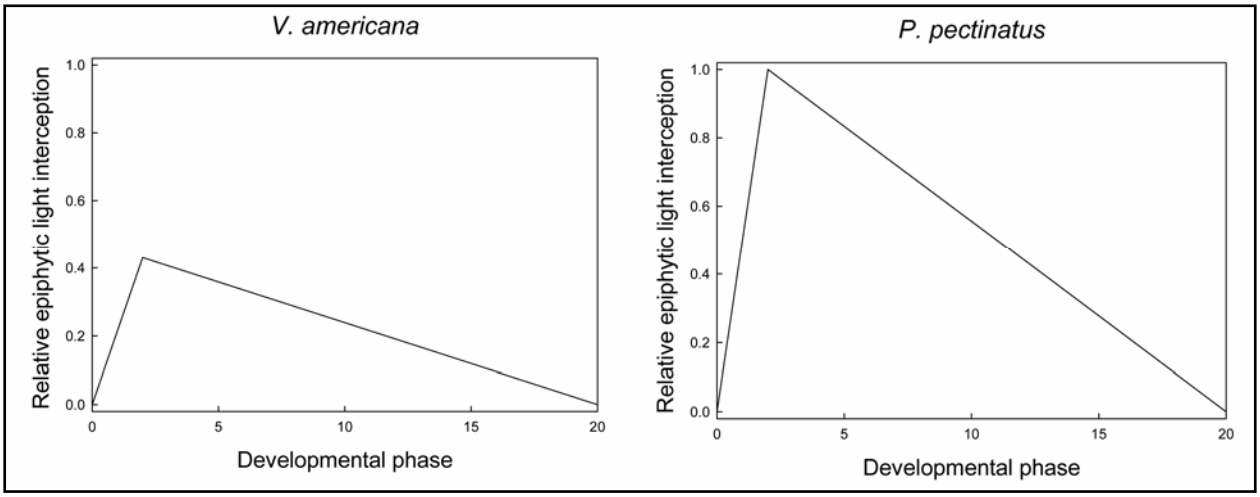

Figure 3. Relationship between developmental phase and relative epiphytic light interception used for model calibration

MODEL RUNS: All four expanded models were tested by repeating the calibration runs of the original models (version 1.0). The results of the calibration runs matched those of the original models (data not shown).

Plant growth is greatly affected by climate: timing and development rate of phenological cycle by temperature-dependent degree-day sum and day length, gross photosynthesis by irradiation and temperature, and respiration by temperature (biomass production = gross production – respiration). The effects of climate on phenological cycle are decisive for the geographical distribution of plant species. Figure 4 illustrates these effects, where the flowering phase (development phase DVS=1) is reached on 3 August (Julian dayno 215) in a temperate climate but on 6 March (Julian dayno 65) in a tropical climate in *Vallisneria* species.

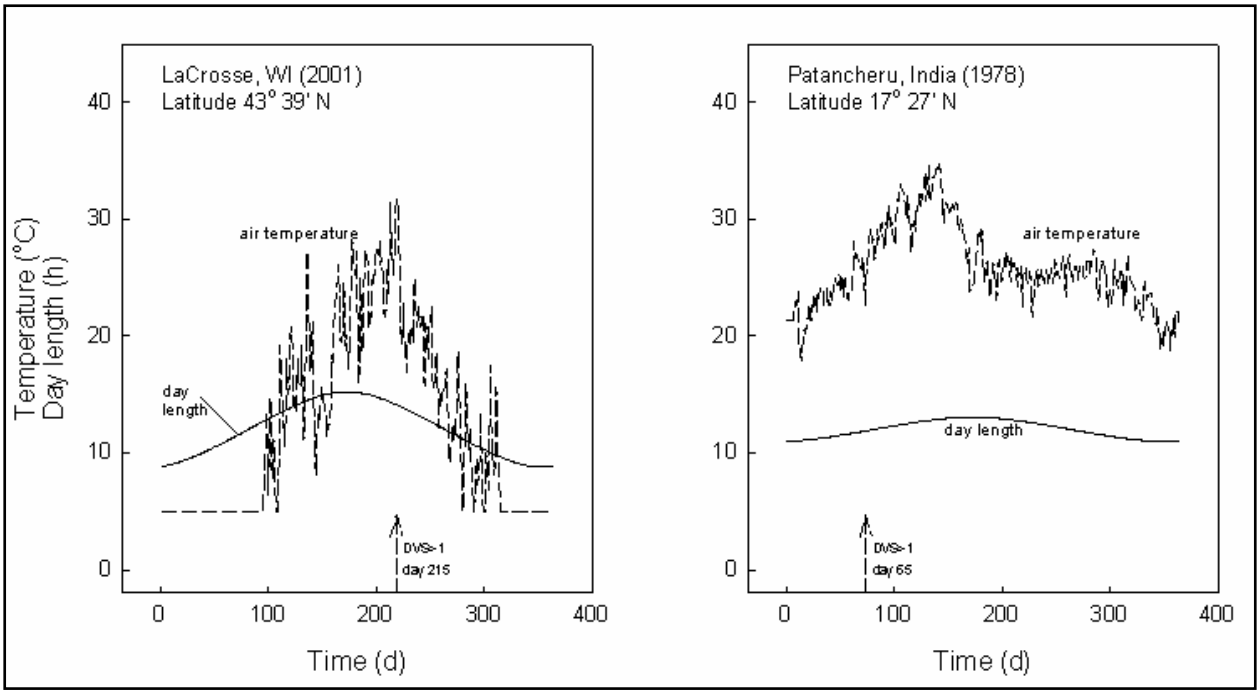

Figure 4. Day length and average temperature in a temperate (left) and tropical (right) climates. Flowering, indicated by DVS=1, occurs later in a temperate than in a tropical climate. Weather conditions: temperate, LaCrosse, WI, USA, 2001; tropical, Patancheru, India, 1978.

Therefore, the models were also tested by conducting two runs for SAV at similar sites in a temperate (LaCrosse, WI, USA; 2001) and a tropical (Patancheru, India; 1978) climate. Environmental conditions were representative for sites in Navigation Pool 8, Upper Mississippi River, LaCrosse, WI, USA, where environmental data were available as inputs and field data on plant biomass collected in 2001 were available for verification of the model outputs of VALLA and POTAM (Best et al. 2005). For VALLA runs the site 'Turtle Island' was used. For POTAM runs the site 'Lawrence Lake' was used. All HYDRIL and MILFO runs were executed using environmental data pertaining to the 'Lawrence Lake' site. Among these sites, the Turtle Island site is characterized by shallow water (depth of 0.2 m at the day of harvest), current velocities tolerable for SAV (ranging from 0.03 to 0.37 m s^{-1}), and high turbidity in the plant growth season (light extinction coefficients ranging from 3.00 to 4.23 m^{-1}). The Lawrence Lake site is characterized by a highly fluctuating water level (0.20 to 1.83 m), low current velocities (ranging from 0 to 0.37 m s^{-1}), and high turbidity in the plant growth period (light extinction coefficients ranging from 1.01 to 4.71 m^{-1}). All runs were conducted for a plant community in a water column measuring 0.5 m depth at the end of July 2001.

Results of a VALLA run performed for the Turtle Island site, EB5B, and a temperate climate in 2001 indicated that simulated shoot biomass at the day of harvest (without and with corrections for epiphyte shading effects) was within the range of the measured shoot biomass, but with corrections for current velocity and both epiphyte shading and current velocity it was below the measured range (Figure 5-upper). All simulated peak shoot biomass values were within the range of the measured values. Peak shoot biomass, without corrections for the effects of current velocity and epiphyte shading, was similar to mean shoot biomass measured at the day of harvest, but was about 30 days delayed in time. Peak biomass generated by runs corrected for

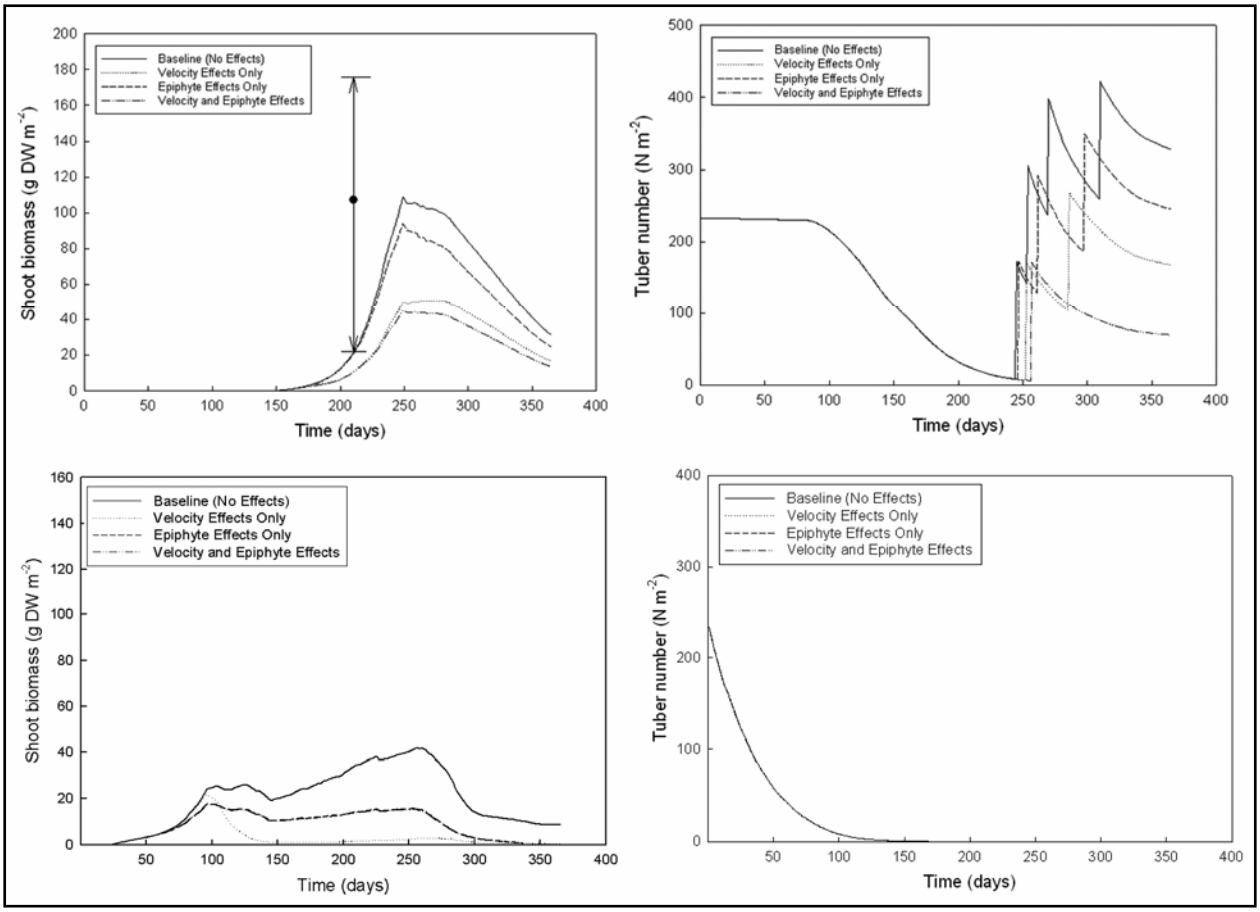

Figure 5. Simulated shoot biomass and tuber number of *V. americana* under temperate (upper) and tropical (lower conditions. Environmental conditions of depth and light extinction within water column, current velocity, and epiphyte shading mimicking those measured in 2001 at field site EB5B Turtle Island of Navigation Pool 8 of the Mississippi River. Initial tuber number = 233 m^{-2} (default). Solid dot indicates shoot biomass measured in the field.

current velocity effects was 50 percent lower, corrected for epiphyte shading 10 percent lower, and corrected for both effects 64 percent lower than peak biomass without corrections. Thus, simulated plant biomass was greatly decreased by on-site current velocity and epiphyte cover. Simulated end-of-year tuber number was always substantial, ranging from 80 to around 350 tubers per m^{-2}. This indicates that the *V. americana* population would persist because the end-of-year tuber number was > 1, and the tuber size was large enough to enable sprouts to become self-supporting in their carbon gain at shallow sites (0.5-m depth at relatively turbid water common in the UMR) (Best et al. 2005). In a tropical climate, simulated shoot biomass would be lower, two plant cohorts would develop and grow, but tuber formation would not occur (Figure 5-lower). The viability of SAV tubers varies among species, and is relatively short for *V. americana* and *P. pectinatus*, i.e., about 9 months (Titus and Stephens 1983, Van Wijk 1989), but can be far longer, i.e., three years in *H. verticillata*.[1] Tuber formation in several SAV species, such as *V. americana*, and *P. pectinatus*, is initiated by a combination of a relatively short day length and a

[1] Personal communication. 1995. D. L. Sutton, PhD, Center for Aquatic Weeds, University of Florida, Fort Lauderdale, FL.

high temperature. Because this combination did not occur in the tropical climate used for the model runs, simulated tubers were not formed. Under these conditions plants would re-grow from wintering shoots or from seeds. The lack of tuber formation in these species in a tropical climate was confirmed by the literature (Sahai and Sinha 1973, Haller 1974).

A POTAM run was performed for the Lawrence Lake site (EB2E) in 2001 with a temperate climate. There was a good match between simulated shoot biomass at the day of harvest and measured shoot biomass, because it was within the range of the measured shoot biomass, uncorrected, corrected for the effects of current velocity and/or epiphyte shading, and corrected for the effects of both factors (Figure 6-upper). Simulated peak biomass exceeded shoot biomass measured at the day of harvest. Decreasing effects of current velocity on shoot biomass were minimal, and effects of epiphyte shading were large, i.e., on the order of 40 percent. End-of-year tuber number was 0 when corrected for epiphyte shading effects, but could amount to 64 tubers per m^{-2} without correction for epiphyte shading (Figure 6-upper). Thus, epiphyte shading would prevent the persistence of the sago pondweed population by the inhibition of tuber production at

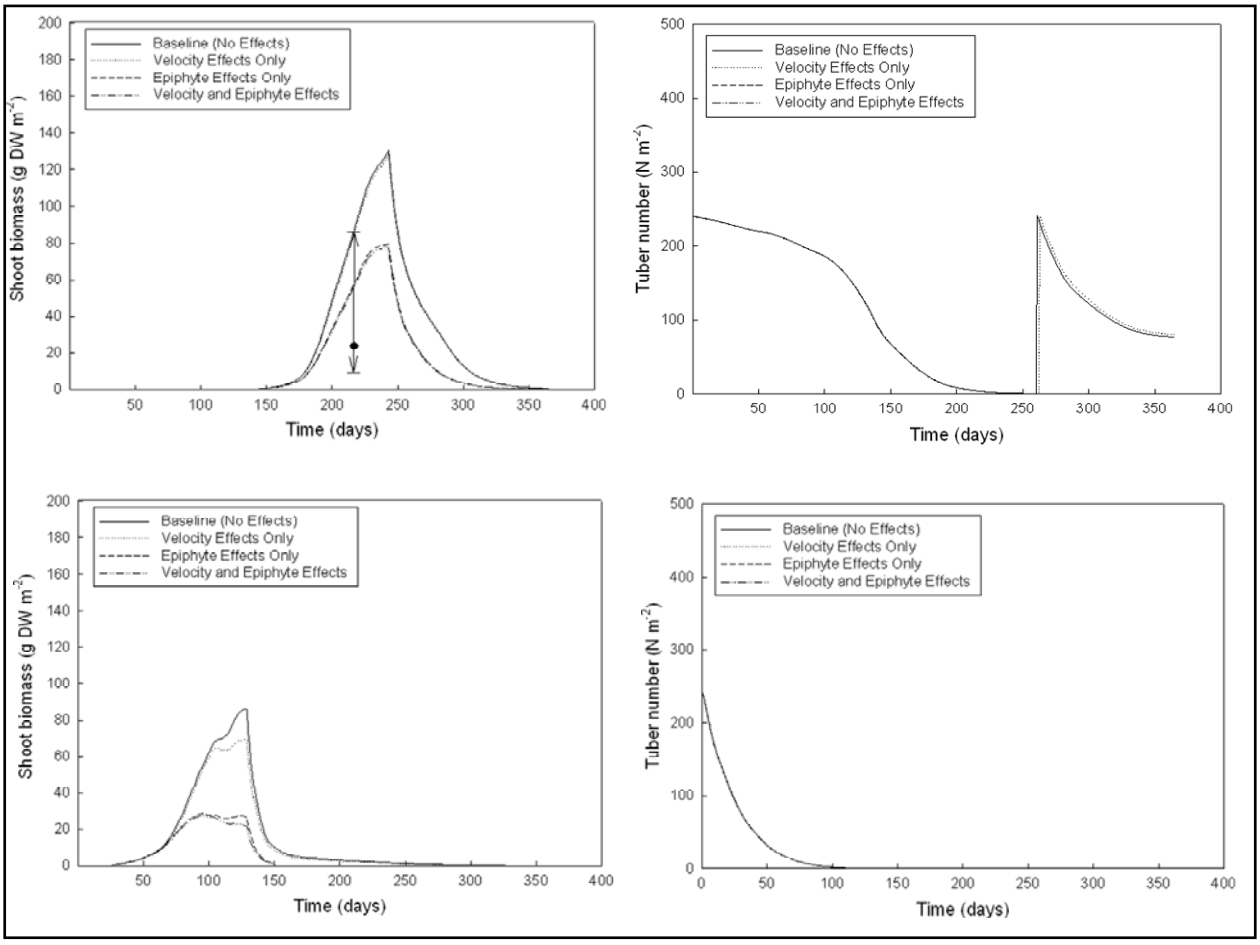

Figure 6. Simulated shoot biomass and tuber number of *P. pectinatus* under temperate (upper) and tropical (lower) conditions. Environmental conditions of depth and light extinction within water column, current velocity, and epiphyte shading mimicking those measured in 2001 at field site EB2E in Lawrence Lake, a backwater of the Mississippi River. Initial tuber number = 240 m^{-2} (default). Solid dot indicates shoot biomass measured in the field.

this site. In a tropical climate, simulated shoot biomass would be far lower, two plant cohorts would develop, grow, and senesce early in the year, and since tuber formation would not occur (Figure 6-lower), this species would only be expected to persist from germinating seeds, once produced.

Results of a HYDRIL run performed for a site mimicking Lawrence Lake site, EB2E, in 2001, and a temperate climate showed the potential for substantial biomass formation relatively late in the season, because growth from tubers started late, i.e. at the end of June, with relatively small decreasing effects of current velocity and/or epiphyte shading (Figure 7-upper). No new tubers were formed, because in the *H. verticillata* biotype for which HYDRIL was calibrated, tubers are initiated at a relatively long day length in combination with a high temperature, and this combination did not occur in this temperate climate. However, end-of-year tuber number was still high, since the simulations started from a relatively high default tuber density of 500 m^{-2}. Despite the fact that such a population could persist for several years because its tubers are viable

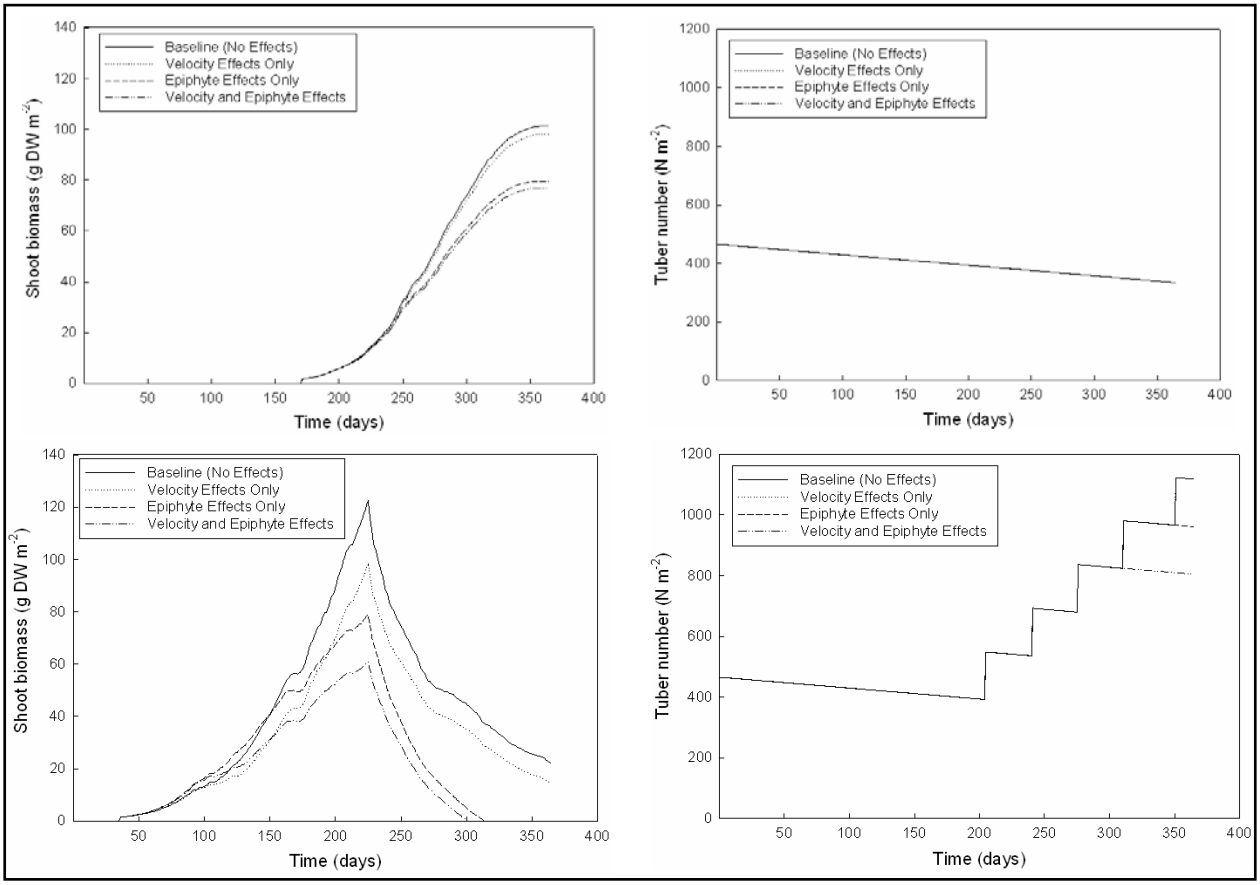

Figure 7. Simulated shoot biomass and tubers of *H. verticillata* under temperate (upper) and tropical (lower) conditions. Environmental conditions of depth and light extinction within the water column, current velocity, and epiphyte shading mimicked those measured in 2001 at field site EB2E in Lawrence Lake, a backwater of the Mississippi River. Initial tuber number = 500 m^{-2} (default).

during such a long period,[1] it is expected to become extinct under environmental conditions in which the aboveground biomass would be removed by natural means (breakage by exposure to strong wind-wave interaction or ice) or management actions (mechanical control). In a tropical climate, simulated shoot biomass would be far higher, two plant cohorts would develop, grow, and senesce over the year, and strong tuber formation would occur (Figure 7-lower) enabling this species to rapidly outcompete other SAV and completely occupy any water body, exhibiting a typical invasive behavior. Experimental evidence published after the development of HYDRIL indicates that all *H. verticillata* biotypes tested (30) can produce tubers at specific long day and temperature combinations, but that local climatological conditions determine whether production actually occurs (Steward 1997).

Results of a MILFO run performed for a site mimicking Lawrence Lake site, EB2E, in 2001, and temperate climate showed the potential for substantial biomass formation peaking at the end of August, with a considerable decreasing effect of epiphyte shading (Figure 8-upper). This species,

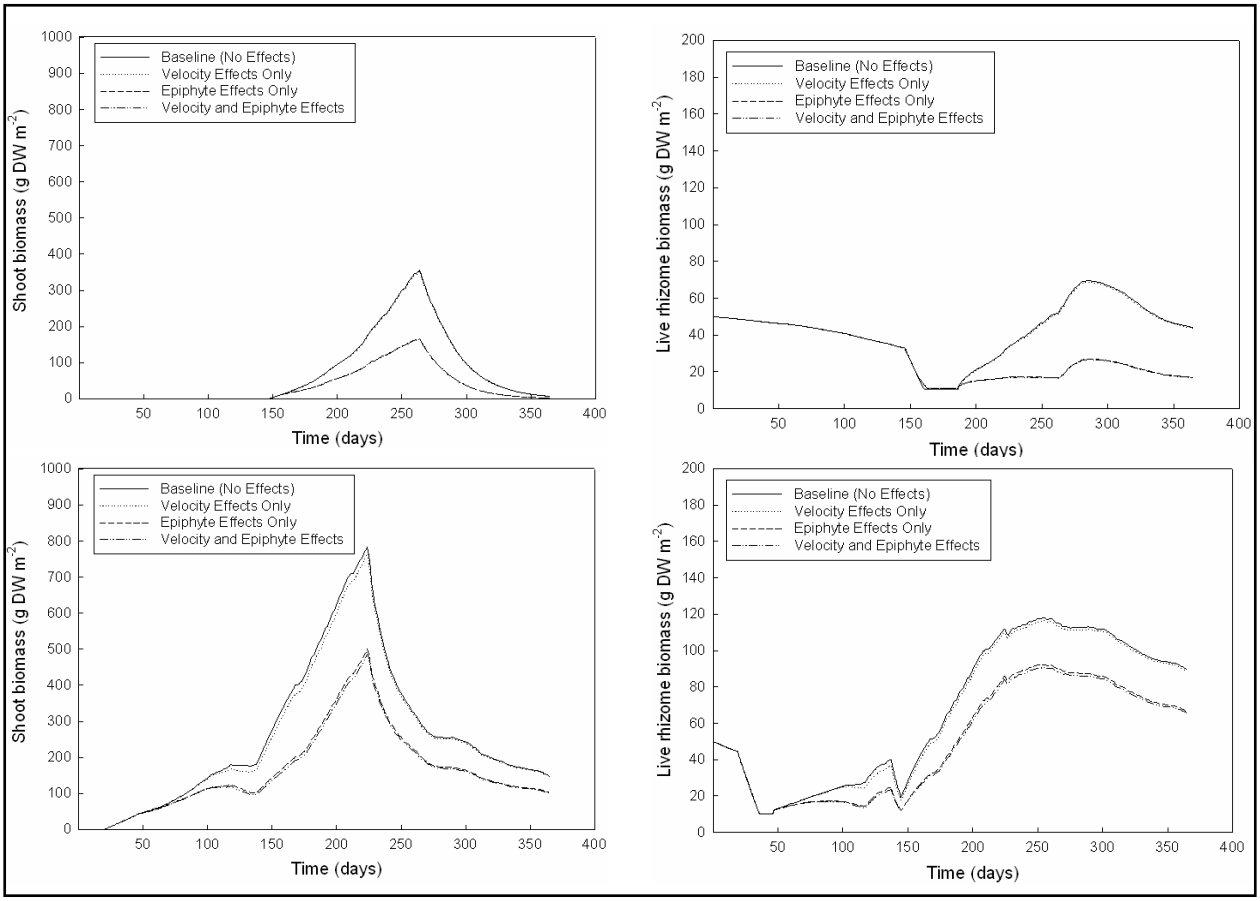

Figure 8. Simulated shoot and live rhizome biomass of *M. spicatum* under temperate (upper) and tropical (lower) conditions. Environmental conditions of depth and light extinction within water column, current velocity, and epiphyte shading mimicking those measured in 2001 at field site EB2E in Lawrence Lake, a backwater of the Mississippi River. Initial rhizome weight = 50 g DW m^{-2} (default).

[1] Personal communication. 1995. D. L. Sutton, PhD, Center for Aquatic Weeds, University of Florida, Fort Lauderdale, FL.

which does not form subterranean tubers, and may winter as rhizomes/root crowns, formed a substantial rhizome mass, sufficient for regrowth the subsequent year. In a tropical climate, simulated shoot biomass would be far higher, two plant cohorts would develop, grow, and senesce over the year, and strong rhizome formation would occur (Figure 8-lower), enabling this species to compete successfully with other SAV and occupy any water body, exhibiting a potentially invasive behavior.

SUMMARY: Simulation models for growth of four submersed aquatic vegetation (SAV) types have been modified in such a way so as to greatly expand their application potential. The modifications include descriptions of the vegetation responses to daily changes in current velocity and epiphyte shading, and accommodation of daily changes in water level. These models can be used to evaluate key environmental conditions in which SAV would persist under a variety of changes in environmental conditions, natural and anthropogenic (frequent changes in water level, flow, water transparency—e.g. due to eutrophication and/or siltation) and management (mechanical removal of portions of above- or below-ground plant organs and grazing by waterfowl). The expanded models have been tested by repeating calibration runs, and conducting new runs under temperate and tropical conditions. The models are available as stand-alone versions, and can be used singly and in combination with hydrodynamic and sediment transport models.

PRODUCT DEVELOPMENT AND AVAILABILITY: The aquatic plant growth models are available to both U.S. Army Corps of Engineers (USACE) and non-USACE interested parties. Versions 1.0 and 3.0 can be downloaded from the following URL: *http://el.erdc.usace.army.mil/products.cfm?Topic=model&Type=aquatic*. Model descriptions and user manuals for Version 1.0 can be downloaded from the same Web page.

POINTS OF CONTACT: This technical note was prepared by Elly P. H. Best and William A. Boyd, research biologists, U.S. Army Engineer Research and Development Center, Environmental Laboratory. The models were upgraded under the Ecological Model Development Work Unit of the System-Wide Water Resources Program (SWWRP). For information on SWWRP, please access *https://swwrp.usace.army.mil/* or contact the Program Manager, Dr. Steven L. Ashby at *Steven.L.Ashby@erdc.usace.army.mil*. Questions about this technical note may be addressed to Dr. Best at (601-634-4246; *Elly.P.Best@erdc.usace.army.mil*). This technical note should be cited as follows:

> Best, E. P. H., and W. A. Boyd. 2007. Expanded simulation models (Version 3.0) for growth of the submersed aquatic plants American wildcelery, sago pondweed, hydrilla, and Eurasian watermilfoil. ERDC TN-SWRRP-07-10, Vicksburg, MS: U.S. Army Engineer Research and Development Center. *https://swwrp.usace.army.mil/*

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Appendix A

Table A1
Parameter values used in VALLA

Parameter	Name	Value	Reference
Morphology, phenological cycle, and development			
Fraction of total dry matter increase allocated to leaves	FLV(T)	0.718	1, 2
Fraction of total dry matter increase allocated to stems	FST(T)	0.159	1, 2
Fraction of total dry matter increase allocated to roots	FRT(T)	0.123	1, 2
Development rate as function of temperature*	DVRV	0.015 d^{-1}	Calibrated
DVR prior to flowering DVRV, subsequently DVRR	DVRR	0.040 d^{-1}	Calibrated
Plant density and maximum plant biomass			
Plant density	NPL	30 m^{-2}	1
Maximum plant biomass		496 g DW m^{-2}	2
Wintering, sprouting, and growth of sprouts to water surface			
Dormant tuber density	NDTUB	233 m^{-2}	3
Tuber size	INTUB	0.090 g DW $tuber^{-1}$	3, 4
Rel. tuber death rate (on number basis)	RDTU	0.018 d^{-1}	1
Rel. conversion rate of tuber into plant material	ROC	0.0576 g CH_2O. g^{-1} DW d^{-1}	5
Relation coefficient tuber weight-stem length	RCSHST	12 m g^{-1} DW	5, 6
Critical shoot weight per 0.1-m depth layer	CRIFAC	0.0091g DW (0.1-m depth layer)$^{-1}$$plnt^{-1}$	3, 4
Survival period for sprouts without net photosynthesis	SURPER	23 d	7,8
Light, photosynthesis, maintenance, growth, and assimilate partitioning			
Plant species specific light extinction coefficient	K(T)	0.0235m^2 g^{-1} DW	9
Fraction of irradiation shaded by epiphytes*	EPISHD	0-0.43	10
Potential CO_2 assimilation rate at light saturation for shoots	AMX	0.0165 g CO_2. g^{-1} DW h^{-1}	9
Initial light use efficiency for shoots	EE	0.000011 g CO_2 J^{-1}	11
Rel. reduction factor for AMX to account for senescence plant parts	REDF(T)	1.0	User def.
Reduction factor to relate AMX to water pH	REDAM	1	
Daytime temperature effect on AMX as function of DVS*	AMTMP(T)	0-1	12
Rel. factor to relate AMX to water current velocity*	REDAM1	0-1	10
Dry matter allocation to each plant layer*	DMPC	0-1	9
Flowering, translocation, senescence, and formation of wintering organs			
Max. relative tuber growth rate (part of net photosynthetic rate)	RTR	0.247 d^{-1}	4, 12,13
Conversion factor for translocated dry matter into CH_2O	CVT	1.05	11
Tuber number concurrently initiated per plant	NINTUB	5.5 $plant^{-1}$	13
Total critical dry weight of new tubers	TWCTUB	14.85 g DW m^{-2}	1, 3,13
Rel. death rate of leaves (on DW basis; Q10=2)	RDR(T)	0.021 d^{-1}	1
Rel. death rate of stems and roots (on DW basis; Q10=2)	RDS(T)	0.021 d^{-1}	1
Site information			
Water depth (field site)	DPT(T)	1.4 m	User def.
Daily water temperature (field site)	WTMP(T)	-, ^oC	User def.
Water type specific light extinction coefficient (field site)	L(T)	0.43-0.80 m^{-1}	1
Water type specific current velocity (field site)	WVEL	0-100 cm s^{-1}	User def.
Total live dry weight measured (field site)	TGWM(T)	-, g DM m^{-2}	User def.
Tuber density measured (field site)	NTM(T)	233 m^{-2}	1

Harvesting			
Harvesting	HAR	0 or 1	User def.
Harvesting day number	HARDAY	1-365	User def.
Harvesting depth (measured from water surface; 1-5 m)	HARDEP	0.1m<DEPTH	User def.

1. Titus and Stephens 1983; 2. Haller 1974; 3. Korschgen and Green 1988; 4. Korschgen et al. 1997; 5. Bowes et al. 1979; 6. Best and Boyd 1996; 7. Titus and Adams 1979b; 8. Best and Boyd 2003c; 9. Titus and Adams 1979a; 10. Best et al. 2005; 11. Penning de Vries and Van Laar 1982 a, b; 12. Donnermeyer1982; 13. Donnermeyer and Smart1985; * Calibration function.

Table A2
Parameter values used in POTAM

Parameter	Name	Value	Reference
Morphology, phenological cycle, and development			
Fraction of total dry matter increase allocated to leaves	FLV(T)	0.731	1,2
Fraction of total dry matter increase allocated to stems	FST(T)	0.183	1,2
Fraction of total dry matter increase allocated to roots	FRT(T)	0.086	1
Development rate as function of temperature *	DVRV	0.015 d^{-1}	Calibrated
DVR prior to flowering DVRV, subsequently DVRR	DVRR	0.040 d-1	Calibrated
Plant density and maximum plant biomass			
Plant density	NPL	30 m^{-2}	1,3
Maximum plant biomass		1,952 g DW m^{-2}	4
Wintering, sprouting, and growth of sprouts to water surface			
Dormant tuber density	NDTUB	240 m^{-2}	1
Tuber size	INTUB	0.083 g DW $tuber^{-1}$	1
Rel. tuber death rate (on number basis)	RDTU	0.026 d^{-1}	5
Rel. conversion rate of tuber into plant material	ROC	0.0576 g CH_2O. g^{-1} DW d^{-1}	6
Relation coefficient tuber weight-stem length	RCSHST	12 m g^{-1} DW	6,7,8
Critical shoot weight per 0.1-m depth layer	CRIFAC	0.0076 g DW (0.1-m depth layer)$^{-1}$ $plnt^{-1}$	7,8
Survival period for sprouts without net photosynthesis	SURPER	27 d	1
Light, photosynthesis, maintenance, growth and assimilate partitioning			
Plant species specific light extinction coefficient	K(T)	0.095 m^2 g^{-1} DW	1
Fraction of irradiance shaded by epiphytes*	EPISHD	0-1.0	9
Potential CO_2 assimilation rate at light saturation for shoots	AMX	0.019 g CO_2. g^{-1} DW h^{-1}	10
Initial light use efficiency for shoots	EE	0.000011 g CO_2 J^{-1}	11
Rel. reduction factor for AMX to account for senescence plant parts	REDF(T)	1.0	User def.
Reduction factor to relate AMX to water pH	REDAM	1	1
Daytime temperature effect on AMX as function of DVS*	AMTMP(T)	0-1	1
Rel. factor to relate AMX to water current velocity*	REDAM1	0-1	9
Dry matter allocation to each plant layer*	DMPC	0-1	1
Flowering, translocation, senescence, and formation of wintering organs			
Max. rel. tuber growth rate (part of net photosynthetic rate)	RTR	0.19	1, 12
Conversion factor for translocated dry matter into CH_2O	CVT	1.05	11
Tuber number concurrently initiated per plant	NINTUB	8 $plant^{-1}$	1,8
Total critical dry weight of new tubers	TWCTUB	19.92 g DW m^{-2}	1,3
Relative death rate of leaves (on DW basis; Q10 =2)	RDR(T)	0.047 d^{-1}	1
Relative death rate of stems and roots (on DW basis; Q10=2)	RDS(T)	0.047 d^{-1}	1
Site information			
Water depth (field site)	DPT(T)	1.3 m	User def.
Daily water temperature (field site)	WTMP(T)	-, ^oC	User def.
Water type specific light extinction coefficient (field site)	L(T)	1.07 m^{-1}	1
Water type specific current velocity (field site)	WVEL	0-100 cm s^{-1}	User def.
Total live dry weight measured (field site)	TGWM(T)	-, g DM m^{-2}	User def.
Tuber density measured (field site)	NTM(T)	440 m^{-2}	3
Harvesting			
Harvesting	HAR	0 or 1	User def.
Harvesting day number	HARDAY	1-365	User def.
Harvesting depth (measured from water surface; 1-5 m)	HARDEP	0.1m<DEPTH	User def.

1.Best and Boyd 2003c; 2. Sher Kaul et al. 1995; 3. Van Wijk 1989; 4. Howard-Williams 1978; 5. Van Wijk 1988; 6. Best and Boyd 1996; 7. Spencer 1987; 8. Spencer and Anderson 1987; 9. Best et al. 2005; 10. Van der Bijl et al. 1989; 11. Penning de Vries and Van Laar 1982a, b; 12. Van Wijk 1988; * Calibration function.

Table A3
Parameter values used in HYDRIL

Parameter	Name	Value	Reference
Morphology, phenological cycle and development			
Fraction of total dry matter increase allocated to leaves	FLV(T)	0.34	1, 2, 3
Fraction of total dry matter increase allocated to stems	FST(T)	0.60	1, 2, 3
Fraction of total dry matter increase allocated to roots	FRT(T)	0.06	1, 2, 3
Development rate as function of temperature*	DVRV	0.012 d^{-1}	Calibrated
DVR prior to flowering DVRV, subsequently DVRR	DVRR	0.012 d^{-1}	Calibrated
Plant density and maximum plant biomass			
Plant density	NPL	35 m^{-2}	4, 5
Maximum plant biomass		900 g DW m^{-2}	4
Wintering, sprouting, and growth of sprouts to water surface			
Dormant tuber density	NT	500 m^{-2}	4
Tuber size	INTUB	0.1 g DW $tuber^{-1}$	6
Rel. tuber death rate (on number basis)	RDTU	0.36 d^{-1}	7
Rel. conversion rate of tuber into plant material	ROC	0.0576 g CH_2O. g^{-1} DW d^{-1}	8
Relation coefficient tuber weight-stem length	RCSHST	12 m g DW^{-1}	3, 8
Light, photosynthesis, maintenance, growth and assimilate partitioning			
Plant species specific light extinction coefficient	K	0.01m^2 g^{-1} DW	4, 9
Fraction of irradiation shaded by epiphytes*	EPISHD	0-0.43	10
Potential CO_2 assimilation rate at light saturation for shoots	AMX	0.0158 g CO_2. g^{-1} DW h^{-1}	4,11
Initial light use efficiency for shoots	EE	0.000011 g CO_2 J^{-1}	12
Rel. reduction factor for AMX to account for senescence plant parts	REDF(T)	1.0	User def.
Reduction factor to relate AMX to water pH	REDAM	0.581	4,13
Daytime temperature effect on AMX as function of DVS*	AMTMP(T)	0-1	13
Rel. factor to relate AMX to water current velocity*	REDAM1	0-1	10
Dry matter allocation to each plant layer*	DMPC	0-1	4, 14
Flowering, translocation, senescence, and formation of wintering organs			
Max. relative tuber growth rate (part of net photosynthetic rate)	RTR	0.4 d^{-1}	15
Conversion factor for translocated dry matter into CH_2O	CVT	1.1	12
Tuber number concurrently initiated per plant	NINTUB	7 $plant^{-1}$	4
Total critical weight new tubers	TWCTUB	24.5 g DW m^{-2}	4,6
Rel. death rate of leaves (on DW basis)	RDR(T)	0.033 d^{-1}	8
Rel. death rate of stems and roots (on DW basis)	RDS(T)	0.033 d^{-1}	8
Site information			
Water depth (field site)	DPT(T)	1.0 m	User def.
Daily water temperature (field site)	WTMP(T)	-, ^oC	User def.
Water type specific light extinction coefficient (field site)	L(T)	0.83 m^{-1}	1, 4
Water type specific current velocity (field site)	WVEL	0-100 cm s^{-1}	User def.
Total live dry weight measured (field site)	TGWM(T)	-, g DW m^{-2}	User def.
Tuber bank density measured (field site)	NTM(T)	500 m^{-2}	8
Harvesting			
Harvesting	HAR	0 or 1	User def.
Harvesting day number	HARDAY	1-365	User def.
Harvesting depth (measured from water surface; 1-5 m)	HARDEP	0.1m<DEPTH	User def.

1. Haller and Sutton 1975; 2. Van et al. 1978b; 3. Van der Zweerde 1981; 4. Bowes et al. 1979; 5. Barko and Smart 1981; 6. Van et al. 1977; 7. Sutton, pers.comm., 1995; 8. Bowes et al. 1977; 9. Ikusima 1970; 10. Best et al. 2005. 11. Van et al. 1978a; 12. Penning de Vries and Van Laar 1982a, b; 13. Van et al. 1976; 14. Ambasht and Ram 1976; 15. Haller et al. 1976;
* Calibration function

Table A4
Parameter values used in MILFO

Parameter	Name	Value	Reference
Morphology, phenological cycle and development			
Fraction of total dry matter increase allocated to leaves	FLV(T)	0.47	1
Fraction of total dry matter increase allocated to roots	FRT(T)	0.06	1
Fraction of total dry matter increase allocated to stems	FST(T)	0.47	1
Development rate as function of temperature	DVRV	0.015 d^{-1}	Calibrated
DVR prior to flowering DVRV, subsequently DVRR	DVRR	0.022 d^{-1}	Calibrated
Maximum plant density and plant biomass			
Plant density	NPL	11 m^{-2}	2
Maximum plant biomass		2,283 g DW m^{-2}	2
Wintering and sprouting of rhizomes/root crowns, and growth of sprouts to water surface			
Initial rhizome weight	IWGRIZ	50 g DW m^{-2}	3
Rel. rhizome death rate	RDRIZ	0.00042 d^{-1}	4
Rel. conversion rate of rhizome weight into plant material	ROC	0.0576 g CH_2O. g^{-1} DW d^{-1}	5
Relation coefficient rhizome/root crown weight-stem length	RCSHST	12 m g DW^{-1}	5, 6
Critical rhizome weight	CRRIZ	12 g DW m^{-2}	7
Light, photosynthesis, maintenance, growth and assimilate partitioning			
Plant species specific light extinction coefficient	K(T)	0.006 m^2 g^{-1} DW	8
Fraction of irradiation shaded by epiphytes*	EPISHD	0-0.43	9
Potential CO_2 assimilation rate at light saturation for shoot tips	AMX	0.0165 g CO_2. g^{-1} DW h^{-1}	10, 11
Initial light use efficiency for shoot tips	EE	0.000011 g CO_2 J^{-1}	12
Rel. reduction factor for AMX to account for senescence plant parts	REDF(T)	1.0	User def.
Reduction factor to relate AMX to water pH	REDAM	0.5	13, 14
Daytime temperature effect on AMX as function of DVS	AMTMP(T)	0 -1	8, 15
Rel. factor to relate AMX to water current velocity*	REDAM1	0-0.43	9
Dry matter allocation to each plant layer	DMPC(T)	0 -1	1
Flowering, translocation, senescence, and formation of wintering organs			
Translocation (part of net photosynthetic rate)	TRAFAC	0.35	5
Conversion factor for translocated dry matter into CH_2O	CVT	1.05	12
Rel. death rate of leaves (on DW basis; Q10=2)	RDR(T)	0.042 d^{-1}	10
Rel. death rate of stems and roots (on DW basis; Q10=2)	RDS(T)	0.042 d^{-1}	10
Site information			
Water depth (field site)	DPTT(T)	1.5 m	User def.
Daily water temperature (field site)	WTMP(T)	-, ^oC	User def.
Water type specific light extinction coefficient (field site)	L(T)	1.15 - 2.00 m^{-1}	13
Water type specific current velocity (field site)	WVEL	0-100 cm s^{-1}	User def.
Total live dry weight measured (field site)	TGWM(T)	-, g DW m^{-2}	User def.
Harvesting			
Harvesting	HAR	0 or 1	User def.
Harvesting day number	HARDAY	1-365	User def.
Harvesting depth (measured from water surface in m)	HARDEP	0.1 m<DEPTH	User def.

1. Adams et al. 1974; 2. Budd et al. 1995; 3. Smith and Adams 1986; 4. Vogt et al. 1991; 5. Bowes et al. 1979;
6. Van der Zweerde 1981; 7. Madsen 1997; 8. Titus and Adams 1979a; 9. Best et al. 2005; 10. Adams and McCracken 1974;
11. Van et al. 1976; 12. Penning de Vries and Van Laar 1982a, b; 13. Lee and Kluesener 1972; 14. Titus and Stone 1982;
15. Stanley and Nailor 1972; 16. Kooman 1995; * Calibration function.